



ORIGINAL  
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# Contrasting responses to water deficits of *Nothofagus* species from tropical New Guinea and high-latitude temperate forests: can rainfall regimes constrain latitudinal range?

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## ABSTRACT

**Aim** Comparative responses of *Nothofagus* species to water deficits were studied to determine whether rainfall regimes could limit the latitudinal ranges of tropical and temperate forest species.

**Location** The study species are native to New Guinea, New Caledonia, Australia, New Zealand, Chile and Argentina.

**Methods** Seedlings of *Nothofagus* species from a broad latitudinal range were grown in a common environment. Changes in conductance, relative water content and water potential were measured in detached shoots, and together with measurements of tissue injury and biomass allocation, were compared between tropical and temperate species.

**Results** Differences in responses to water deficits between tropical and temperate species appear to reflect differences in climate regimes. In particular, species native to ever-wet rainfall regimes in New Guinea, where water deficits are generally likely to be short-lived, were effective at conserving water by reduced stomatal conductance. In contrast, high-latitude evergreen species on average showed greater development of traits that should enhance water uptake. This was particularly evident in *Nothofagus cunninghamii* from southern Australia, which developed low water potentials at moderate levels of tissue water deficit and higher root:leaf biomass than tropical species, potentially allowing carbon assimilation to be maximized during warmer, but drier, summer months. However, water relations varied among high-latitude species. In particular, deciduous species on average showed higher rates of conductance, even during moderate levels of tissue water deficit, than evergreen species.

**Main conclusions** The tropical species appear to conserve water during periods of water deficit (relative to temperate species), which is unlikely to have substantial opportunity costs for growth in ever-wet climates. However, spread of tropical species to higher latitudes may be limited by water conservation strategies that limit carbon gain in climates in which temperature seasonality is often paired with drier summers. Evergreen species from high latitudes, such as *N. cunninghamii*, commonly showed traits that should increase water uptake. However, this strategy, while probably maximizing growth in temperate climates with cool winters and drier summers, must limit competitiveness at lower latitudes in summer-wet climates. We conclude that responses to water regimes may make a significant contribution to the latitudinal limits of some evergreen rain forest species.

## Keywords

Deciduous, drought resistance, evergreen, *Nothofagus*, temperate rain forest, tropical rain forest, vegetation zonation, water relations.

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## INTRODUCTION

Tropical and temperate climates differ substantially, yet relatively little is known about how plants of particular vegetation formations have responded adaptively to these differences. Emphasis has been placed on the role of temperature regimes in explaining the distributional limits of physiognomic forms of vegetation (e.g. tropical forest versus temperate broad-leaved evergreen forest versus broad-leaved deciduous forest) along latitudinal gradients (Woodward, 1987). For example, responses of tropical and temperate species to temperature have been compared in terms of growth (Cunningham & Read, 2003a), photosynthesis (Read, 1990; Cunningham & Read, 2002, 2003b) and frost resistance (Sakai, 1978; Read & Hope, 1989; Cunningham & Read, 2006). Less attention has been given to responses to moisture regimes (other than geographic trends in carbon fixation cycles) (Franks & Farquhar, 1999; Park & Furukawa, 1999; Cunningham, 2004, 2005), even though the sensitivity of rain forest species to drought is well known (Engelbrecht *et al.*, 2007), and despite regimes of rainfall, and more specifically water availability, varying along latitudinal gradients in some regions (Cunningham, 2004).

For the rain forests of eastern Australia and New Guinea (here referring to the West Papuan region of Indonesia plus Papua New Guinea), one of the marked changes with respect to latitude is the shift from winter-high rainfall in southern Australia to summer-high rainfall at mid-latitudes and effectively ever-wet conditions at low latitudes (Table 1). This trend, together with the strong seasonality of temperature (Table 1), may lead to a greater likelihood of water deficits in high-latitude rain forests than in rain forests of lower latitudes. Little is known about how rain forest species may have adapted to these contrasting water regimes. Substantial changes in distributions of rain forest taxa occurred in Australia from the mid-Miocene when temperature and rainfall regimes were changing substantially (Truswell, 1993; McGowran *et al.*, 2000). The distributional changes included massive constriction of rain forest and also shifts in latitudinal ranges of some

rain forest taxa, including the loss from southern Australia of taxa such as *Nothofagus* subgenus *Brassospora* that are now restricted to the tropics (Truswell, 1993; Kershaw *et al.*, 1994; McGowran *et al.*, 2000; Hill, 2001). Such shifts may have been influenced by changing rainfall regimes, in addition to the changing temperature regimes.

A thorough appreciation of adaptations to climate regimes should contribute substantially to our understanding of controls of vegetation zonation, and improve predictions of vegetation responses to future climate changes (Engelbrecht *et al.*, 2007). *Nothofagus* (Nothofagaceae) is useful for such studies because of its relatively detailed fossil record (Hill, 2001), wide latitudinal range (c. 0–55° S), and similar niche as a rain forest canopy tree across much of its geographic range (Veblen *et al.*, 1996a). In Australia, *Nothofagus* is typically restricted to areas of high and relatively reliable rainfall in Tasmania and eastern mainland Australia to a northern limit of c. 28° S (Read & Brown, 1996) and reaches tropical latitudes in New Caledonia and nearly to the equator in montane New Guinea (Read & Hope, 1996). Long-term water-use efficiency (estimated by <sup>13</sup>C discrimination) has been shown to vary in seedlings of *Nothofagus* species from contrasting latitudes that were grown in a common environment, with higher water-use efficiency in tropical species (Read & Farquhar, 1991). The high water-use efficiency in New Guinea species seems paradoxical given that they occur in a very wet climate, with high rainfall on average even in the 'dry' season (Table 1). However, this trend may be due to the efficiency of using stomatal closure to avoid tissue water deficits in a climate where water stress is generally short-lived (Read & Farquhar, 1991). For example, mean hottest month maximum temperatures of climate profiles appear to differ little between New Guinea species and *Nothofagus cunninghamii*, native to southeastern Australia, but the former experience higher rainfall (Table 1) and humidity and so probably lower vapour pressure deficits. Hence, such a strategy might not be costly compared with alternative strategies such as increasing root biomass at the expense of leaf growth.

**Table 1** Descriptive statistics for climate variables for evergreen *Nothofagus* species from tropical New Guinea (all species combined), *N. moorei* from mid-latitudes in Australia and *N. cunninghamii* from high latitudes in Australia. Temperature variables are given in °C, and precipitation in mm, with the mean ± standard deviation (5th–95th percentile in brackets) for *n* location records. The estimates were derived by BIOCLIM (Nix, 1986) and ANUCLIM v. 5.0 (Houlder *et al.*, 1999) (see text). Seasonal temperature range is calculated as the hottest month mean temperature minus the coldest month mean temperature. Precipitation seasonality is the coefficient of variation.

Climate variable	New Guinea species ( <i>n</i> = 301)	<i>N. moorei</i> ( <i>n</i> = 139)	<i>N. cunninghamii</i> ( <i>n</i> = 318)
Annual mean temperature	16.1 ± 2.9 (12.0–21.5)	12.2 ± 1.4 (10.1–14.6)	9.5 ± 2.0 (5.8–12.4)
Hottest month max. temp.	21.4 ± 3.1 (16.5–27.2)	23.2 ± 1.4 (21.0–25.7)	20.8 ± 2.8 (15.9–25.3)
Coldest month min. temp.	10.7 ± 3.0 (6.9–16.4)	0.9 ± 1.6 (–0.9–5.1)	1.6 ± 1.8 (–1.5–4.2)
Seasonal temperature range	1.3 ± 0.8 (0.8–1.9)	12.4 ± 0.8 (10.8–13.4)	10.3 ± 1.6 (7.9–12.8)
Annual precipitation	2891 ± 743 (2073–4439)	1633 ± 325 (1229–2282)	1816 ± 523 (1127–2950)
Precipitation of hottest quarter	888 ± 249 (666–1159)	564 ± 142 (390–844)	304 ± 92 (191–516)
Precipitation of coldest quarter	526 ± 254 (301–1069)	315 ± 49 (232–388)	551 ± 158 (351–887)
Precipitation of wettest quarter	955 ± 348 (689–1491)	611 ± 179 (396–959)	570 ± 160 (364–899)
Precipitation of driest quarter	474 ± 166 (301–869)	249 ± 35 (194–302)	304 ± 95 (191–516)
Precipitation seasonality	28 ± 11 (14–44)	34 ± 11 (18–46)	25 ± 5 (18–35)

Some *Nothofagus* species from temperate latitudes are probably exposed to drier conditions, even though they occur in rain forest. *Nothofagus cunninghamii*, for example, experiences moist conditions in winter when photosynthesis would be constrained by low temperatures (Read & Busby, 1991), but lower rainfall conditions in summer (Table 1) when temperatures are more optimal for photosynthesis. Although average summer rainfall is relatively high (Table 1) it can be considerably reduced in drought years, with probable high evaporative demand on warm dry days even in non-drought years. Use of rapid stomatal closure to minimize tissue water deficits in summer may limit photosynthesis and growth too severely, and instead *N. cunninghamii* is predicted to invest more in other mechanisms to maintain tissue water status (Read & Farquhar, 1991). Some of these mechanisms (e.g. root allocation and architecture) may gain efficiency from also addressing deficits in soil nutrients, given the poor soil nutrition across much of the range of this species (Read, 2001). Consistent with this prediction, seedlings of *N. cunninghamii* showed relatively little reduction in stomatal conductance (18% reduction) compared with those of unrelated tropical species (45–85% reduction) at vapour pressure deficits of 1.9 kPa (Cunningham, 2004), with no decrease in rates of net photosynthesis (Cunningham, 2005). *Nothofagus cunninghamii* also develops low osmotic potentials (Somerville & Read, 2008), increasing the capacity to pull water from the soil. It is not clear, however, how this behaviour compares with that of *Nothofagus* species from ever-wet tropical climates grown under the same conditions, or with that of other temperate *Nothofagus* species, particularly with the Australian mid-latitude species *Nothofagus moorei*, which grows in a seasonal temperate climate that experiences wet summers on average (Table 1).

Hence, the primary aim of this study was to determine how temperate *Nothofagus* species differ from tropical species in their response to water deficits. We compared the water relations of seedlings of *Nothofagus* species from a broad latitudinal range grown in a common environment. Specifically, we investigated whether temperate species maintained higher rates of stomatal conductance during periods of water deficits than tropical species, and if so, whether they had compensatory adaptations such as the potential for increased water uptake. In addition, since the temperate group comprises deciduous and evergreen species, a secondary aim was to determine whether these traits differed between species with contrasting leaf habits. To address these aims, we compared variables derived from pressure–volume curves, conductance responses to leaf dehydration, tissue damage resulting from dehydration and root biomass allocation between tropical and temperate species.

## MATERIALS AND METHODS

### Water relations

Plants were raised from young seedlings collected in the field, or from seed. They were grown in a glasshouse in Hobart, Tasmania

(42°54' S, 147°19' E, 60 m a.s.l.), prior to the experiment. The species and level of replication are shown in Table 2. Replication was low in some tropical species because of low seedling survival rates after long-distance transport and quarantine treatment, and in some temperate species due to problems of availability. Although the low level of replication is not ideal, this study generally focuses on differences between functional groups (tropical versus temperate evergreen versus temperate deciduous species) using species as replicates, rather than on species-level differences; caution is used in interpretation of data derived from low levels of replication, and species with low numbers of replicates were not outliers for any traits. The low numbers of available seedlings also limited the type of experiment undertaken. Multiple collection sites of contrasting climate were used in some species to include potential ecotypic variation (Table 2). *Nothofagus aequilateralis* from tropical New Caledonia was included with the tropical species in the conductance experiment. *Castanopsis acuminatissima* (Fagaceae) (collected at the same site in Papua New Guinea as *Nothofagus crenata* var. *sapei*), was included as a tropical comparator in a closely related family, but was not included in statistical analyses.

During the experiments the plants were grown under common conditions in sandy loam soil in individual pots and watered daily, with quarter-strength nutrient (Aquasol®) applied fortnightly. The plants were c. 30 cm high when placed in two growth cabinets, with species replicates spread between the cabinets. The cabinets were maintained at 20 °C day/10 °C night, with a 12-h photoperiod. These temperatures are within the range experienced by tropical and temperate *Nothofagus* species (e.g. Table 1), except for *N. crenata* var. *sapei* which experiences higher average minima (Read *et al.*, 2005). The photosynthetic photon flux density at foliage height was 400–440  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The relative humidity in the cabinets varied from a mean of 77% during the light period to 92% during the dark period. Plants were grown under these conditions for c. 4 months to allow sufficient leaves to develop under these conditions.

### Stomatal conductance, relative water content and tissue damage in detached leaves

Stomatal conductance ( $g_s$ ) was monitored over time on three detached leaves of each of up to three plants per species. Leaves were detached in order to allow measurement of leaf responses under similar conditions of water deficit, i.e. decoupled from access to soil water. A Li-700 transient porometer (LI-COR Biosciences, Lincoln, NE, USA) was used to measure  $g_s$  of attached leaves within 1–2 h of the commencement of the light period (shown in pilot studies to be 98–100% hydrated), then leaves (multiple leaves for small-leaved species) were detached, wrapped in moist tissue and taken to the laboratory and weighed (turgid mass). The leaves were then laid lower-side down on a coarse wire mesh (raised above the bench) and allowed to dehydrate at ambient conditions (c. 21 °C and 43% relative humidity) for 2 h. Stomatal conductance was measured at 20, 40, 60 and 120 min under these conditions. After

**Table 2** List of *Nothofagus* species studied, the subgenus of each and their collection sites. Annual mean temperature and precipitation of collection sites were estimated by BIOCLIM for species from Australia and New Guinea (Table 1) and by WorldClim v. 1.4 (Hijmans *et al.*, 2005a) with DIVA-GIS v. 7 (Hijmans *et al.*, 2005b) for other species, except annual precipitation for South American species, which was taken from Fig. 12 of Prohaska (1976). We note that precipitation may be underestimated by BIOCLIM and WorldClim in some mountainous regions.

Species	<i>n</i>	Collection site	Annual mean temperature (°C)	Annual precipitation (mm)
<b>Tropical</b>				
New Caledonia				
<i>N. aequilateralis</i> (Baum.-Bod.) Steenis (B)	1	Col de Yaté: 22°10' S, 166°52' E, 180 m a.s.l.	21.3	2437
Papua New Guinea				
<i>N. brassii</i> Steenis (B)	2	Onim: 6°10' S, 143°55' E, 2300 m a.s.l.	15.0	3026
<i>N. carrii</i> Steenis (B)	5	Wau: 7°21' S, 146°41' E, 2200 m a.s.l.	14.6	2751
<i>N. crenata</i> var. <i>sapei</i> Steenis (B)	1	Gesege: 6°26' S, 143°26' E, 920 m a.s.l.	22.3	4121
<i>N. grandis</i> Steenis (B)	1	Nurenk: 5°30' S, 144°20' E, 1950 m a.s.l.	16.9	2700
<i>N. pullei</i> Steenis (B)	5	Onim: (as above)	15.0	3026
	2	Tari: 5°57' S, 143°13' E, 2520 m a.s.l.	13.4	2600
<i>N. resinosa</i> Steenis (B)	4	Iwam Pass: 5°50' S, 145°8' E, 2840 m a.s.l.	11.8	2583
<b>Temperate evergreen</b>				
Australia				
<i>N. cunninghamii</i> (Hook.) Oerst. (L)	5	Mt Field (Tas): 42°41' S, 146°38' E, 980 m a.s.l.	5.8	1524
	5	Christmas Hills (Tas): 40°54' S, 145°02' E, 40 m a.s.l.	11.9	1224
	5	Myrtle Bank (Tas): 41°16' S, 147°23' E, 560 m a.s.l.	9.1	1472
	5	Hartz Mts (Tas): 43°12' S, 146°47' E, 600 m a.s.l.	7.7	1612
	2	Mt Donna Buang (Vic): 37°43' S, 145°43' E, 660 m a.s.l.	10.3	1490
	5	Bulga Bulga (Vic): 38°26' S, 146°34' E, 640 m a.s.l.	10.3	1380
	4	Melba Gully (Vic): 38°42' S, 143°22' E, 380 m a.s.l.	11.0	1613
<i>N. moorei</i> (F. Muell.) Krasser (L)	5	Mt Banda Banda: 31°10' S, 152°24' E, 1050 m a.s.l.	12.3	1724
	5	Barrington Tops: 31°57' S, 151°27' E, 1500 m a.s.l.	9.7	1504
	5	Bobo River: 30°13' S, 152°49' E, 500 m a.s.l.*	15.1	1618
Chile				
<i>N. betuloides</i> (Mirbel) Oerst. (N)	3	Antillanca Valley: 40°47' S, 72°13' W, 1000 m a.s.l.	6.1	1953
<i>N. dombeyi</i> (Mirbel) Oerst. (N)	5	Antillanca Valley: 40°47' S, 72°20' W, 820 m a.s.l.	8.1	2244
New Zealand				
<i>N. fusca</i> (Hook.f.) Oerst. (F)	5	Maruia Valley: 41°58' S, 172°15' E, 350 m a.s.l.	9.6	2154
<i>N. menziesii</i> (Hook.f.) Oerst. (L)	5	Springs Junction: 42°18' S, 172°10' E, 350 m a.s.l.	10.2	2069
<i>N. solandri</i> var. <i>cliffortioides</i> (Hook.f.) Poole (F)	5	Mt Thomas: 43°09' S, 172°20' E, 400 m a.s.l.	9.2	1014
<i>N. solandri</i> var. <i>solandri</i> (Hook.f.) Oerst. (F)	5	Mt Thomas: 43°09' S, 172°20' E, 400 m a.s.l.	9.2	1014
<i>N. truncata</i> (Colenso) Cockayne (F)	5	Ahaura: 42°20' S, 171°35' E, 100 m a.s.l.	11.9	2309
<b>Temperate deciduous</b>				
Australia				
<i>N. gunnii</i> (Hook.f.) Oerst. (F)†	1	Mt Field (as above)	5.8	1524
Chile				
<i>N. alessandri</i> Espinosa (F)	2	Cauquenes: 36°5' S, 72° W, 200–250 m a.s.l.	‡	
<i>N. alpina</i> (Poepp. & Endl.) Oerst. (L)	5	San Pablo: 39°33' S, 72°3' W, 810 m a.s.l.	7.7	> 3000 mm
<i>N. antarctica</i> (G. Forster) Oerst. (N)	5	Antillanca Valley: 40°47' S, 72°13' W, 1050 m a.s.l.	6.1	> 3000 mm
<i>N. glauca</i> (Phil.) Krasser (L)	5	Not known		
<i>N. obliqua</i> (Mirbel) Oerst. (L)	5	Not known		
<i>N. pumilio</i> (Poepp. & Endl.) Krasser (N)†	1	Antillanca Valley: 40°47' S, 72°12' W, 1050 m a.s.l.	5.2	> 3000 mm

*n*, number of replicate plants. Subgenera: B, *Brassospora*; F, *Fuscospora*; L, *Lophozonia*; N, *Nothofagus*. *N. aequilateralis*, *N. gunnii* and *N. pumilio* were not included in the pressure–volume experiment. *N. brassii* was incorrectly listed as *N. cf. carrii* and *N. resinosa* was listed as *N. pseudoresinosa* in Read & Farquhar (1991). Vic, Victoria; Tas, Tasmania.

\*These plants were only used for the biomass allocation study.

†This species was only used in the conductance study.

‡Location data were insufficiently precise to allow reliable estimation of climate data.

120 min the leaves were weighed (fresh mass) and oven-dried at 105 °C to constant mass. Relative water content (RWC) was determined as  $100 \times (\text{fresh mass} - \text{dry mass}) / (\text{turgid mass} - \text{dry mass})$ .

Damage resulting from dehydration was measured using the electrical conductivity technique (Hallam & Tibbits, 1988; Read & Hope, 1989), on the assumption that damage would alter the permeability of the cell membrane, resulting in leakage of electrolytes (Dexter *et al.*, 1930). The index of injury,  $I$ , was weighted by the control value (undamaged tissue) for each species so that  $I = 0$  in undamaged tissue and  $I = 100$  in fully damaged tissue (Flint *et al.*, 1967). A trial comparing visually estimated tissue damage with damage assessed by the electrical conductivity technique in *Atherosperma moschatum* Labill. (Atherospermataceae) indicated a strong correlation ( $R = 0.98$ ,  $P < 0.001$ ) between estimation methods and no significant difference in estimates of damage at the tested range of relative water content (45–100%) (J. Read, unpublished data).  $I_t$ , the index of injury resulting from drying for time  $t$ , was calculated as  $100(R_t - R_o) / (1 - R_o)$ ;  $R_t = L_t/L_k$ ;  $R_o = L_o/L_d$ .  $R_t$  is the fractional release of electrolytes from a sample dehydrated for time  $t$ ;  $R_o$  is the fractional release of electrolytes from a fully hydrated sample;  $L_t$  is the specific conductivity of leachate from a sample dehydrated for time  $t$ ;  $L_k$  is the specific conductivity of leachate from a sample dehydrated for time  $t$ , then heat-killed;  $L_o$  is the specific conductivity of leachate from a fully hydrated sample;  $L_d$  is the specific conductivity of leachate from a fully hydrated sample that has been heat-killed (after Flint *et al.*, 1967).

Immediately after measuring leaf fresh mass, three to five discs (5 mm diameter) were punched from each leaf (or multiple small leaves), placed in a vial and 8 mL of distilled water added. The vials were sealed and shaken at room temperature for 24 h, by which time the solution conductivity was stable. Solution electrical conductivity was measured with a Radiometer Copenhagen CDM 3 conductivity meter (type PP1042 RF probe). Samples were then placed in a water bath in a microwave and boiled to completely kill the tissue. Electrical conductivity values obtained were equal to the maximum values obtained after dehydration. The vials were then shaken for 24 h and the solution conductivity remeasured ( $L_k$ , see above) (the discs were then dried to constant mass at 105 °C and the mass included in the determination of whole leaf dry mass for measurement of RWC). Control values were obtained as above, using fully hydrated tissue.

#### Pressure volume curves and tissue damage

Small terminal unshaded shoots <10 cm long (one to five leaves) were collected (within 1 h of the start of the light period, wrapped in moist tissue) to produce a pressure–volume curve for each individual plant, and to determine tissue damage across a range of values of RWC and shoot water potential ( $\Psi$ ). Each data point in the curve represents a separate small shoot, rather than the usual case where a curve is derived from a single drying shoot or leaf. This method

allowed calculation of tissue damage at each level of  $\Psi$  and RWC. At least 10 small shoots were collected per plant.

Water potential was determined following Turner (1981) using a custom-made pressure chamber. Water potential was measured on one shoot immediately after removal from the damp tissue (0–0.2 MPa) and the remaining shoots were allowed to dry at ambient conditions (*c.* 21 °C and 43% relative humidity) for up to 24 h. A shoot was selected randomly at intervals for measurement of  $\Psi$ . A sample of three to five discs of leaf tissue was then immediately punched from one or more leaves, weighed (fresh mass) and floated in a Petri dish of distilled water for 4 h (sufficient for rehydration) under ambient room lighting and then reweighed (turgid mass). Tissue damage was measured using the electrical conductivity technique. No relationship was detected between the capacity of leaf tissue to rehydrate (judged as dry mass:turgid mass) and tissue injury. Discs were then oven-dried to constant mass at 105 °C (dry mass) and RWC calculated. Pressure–volume curves were analysed with the software TEMPLATE (Radford & Lamont, 1992), using RWC calculated as described, to derive osmotic potential at full turgor ( $\Pi_{100}$ ), osmotic potential at the turgor-loss point ( $\Pi_0$ ), relative water content at the turgor-loss point (RWC<sub>0</sub>), percentage bound water ( $B$ ) and the bulk elastic modulus ( $\epsilon$ ) corrected for apoplasmic water.

#### Root biomass allocation

Seedlings of the Australian species, *N. cunninghamii* (two contrasting populations: Hartz Mountains and Bulga Bulga) and *N. moorei* (Bobo River population), and four species from New Guinea (*Nothofagus carrii*, *Nothofagus grandis*, *Nothofagus pullei* and *Nothofagus resinosa*) were grown in pots in sandy loam in a glasshouse at Monash University, Melbourne (37°54' S, 145°8' E, 98 m a.s.l.). Plants were watered daily and quarter-strength Aquasol® was applied monthly. The mean daily maximum temperature was 23.8 °C, with a relative humidity of 54% (average daily minimum) to 88% (average daily maximum). Plants were harvested after 3 months. Leaves were removed from each plant and total leaf area was measured by image analysis (Mix image analysis software, R. Stolk and G. Sanson, Monash University). Leaves, stems and roots were oven-dried at 105 °C to constant mass and weighed.

#### Climate estimates

Climate profiles were estimated by BIOCLIM (Nix, 1986) for evergreen *Nothofagus* species from tropical New Guinea and Australia, updated from Read *et al.* (2005) and Read & Brown (1996), respectively. Additional site locations for *N. moorei* were obtained from the North Coast Regional Botanic Gardens Herbarium and the Department of Environment, Climate Change and Water (NSW) (29 September 2009) and analysed by ANUCLIM v. 5.0 (Houlder *et al.*, 1999). For the other species used in this study, estimates of annual mean temperature and annual precipitation of collections sites were derived by



WorldClim v. 1.4 (30-second resolution) (Hijmans *et al.*, 2005a) with DIVA-GIS v. 7 (Hijmans *et al.*, 2005b).

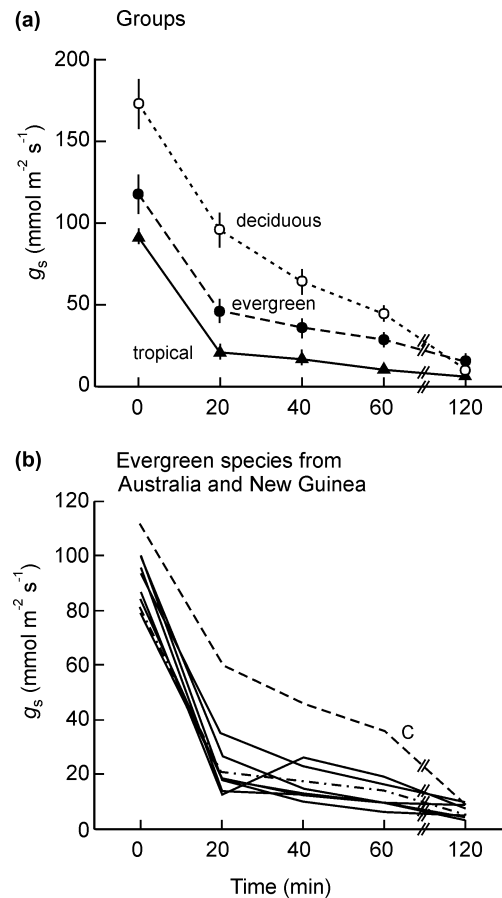
## Data analysis

Two-way ANOVA with repeated measures was used to compare  $g_s$  across the three *Nothofagus* groups (tropical, temperate evergreen and temperate deciduous) and time. Values from subreplicate leaves were averaged for each plant, and plant-level values were then averaged for each species. For species collected from multiple sites or varieties, data were averaged for each site or variety, and then these values were averaged. One-way ANOVA with post hoc Tukey's tests was used to test for differences in RWC and  $I$  among groups at the end of the experiment, with species as replicates. Nonlinear regression was used to fit the Gompertz model ( $y = 100 \{ \exp[-\exp(-b + cx)] \}$ ) to the relationship between  $I$  and RWC in the pressure–volume curve experiment and to derive the relative water content causing 20% ( $RWC_{I-20}$ ) and 50% ( $RWC_{I-50}$ ) damage and the level of damage at  $RWC_0$ . One-way ANOVA with post hoc Tukey's tests was used to test for differences among groups in all variables from this experiment. Pearson correlation was used to test associations among selected variables. Principal components analysis (PCA) was used to summarize trends in water relations variables. Data assumptions were checked for all analyses and transformations used where necessary. A critical value of  $\alpha = 0.05$  was used in hypothesis testing. SYSTAT® v. 12 was used for all analyses.

## RESULTS

### Stomatal conductance ( $g_s$ ), relative water content (RWC) and tissue damage ( $I$ ) in detached leaves

All groups of *Nothofagus* species (tropical, temperate evergreen and temperate deciduous) showed a decline in  $g_s$  during the 2 h dehydration trial ( $F = 218.6$ ,  $P < 0.001$ ), with  $g_s$  differing among groups ( $F = 25.2$ ,  $P < 0.001$ ) and the degree of decline over time varying among groups (interaction term:  $F = 9.9$ ,  $P < 0.001$ ) (Fig. 1). Significant differences were recorded among the three groups in  $g_s$  in the hydrated state ( $g_{s \max}$ ),  $g_s$  during the course of dehydration, and in RWC and tissue damage ( $I_{120-\min}$ ) following the dehydration period (Table 3). The evergreen species had significantly lower  $g_{s \max}$  than the deciduous species, with no significant difference between tropical and temperate evergreen species (Fig. 1a, Table 3). There was a markedly lower  $g_s$  in all groups at 20 min, with groups differing significantly in both  $g_s$  and percentage of maximum  $g_s$  in the order deciduous > temperate evergreen > tropical species (Fig. 1a, Table 3). After 2 h, RWC was more than two times higher in tropical species than deciduous species, with temperate evergreen species having intermediate values (Table 3). Damage was low in the tropical species, five times higher in temperate evergreen species on average and eleven times higher in the deciduous species (Table 3). The percentage reduction in conductance at 20 min



**Figure 1** Changes in conductance ( $g_s$ ) over time in detached leaves of *Nothofagus* species. (a) Tropical ( $n = 6$ ), temperate evergreen ( $n = 9$ ) and temperate deciduous groups ( $n = 7$ ) (replicates are species). (b) Tropical species from New Guinea (*N. brassii*, *N. carrii*, *N. crenata* var. *sapei*, *N. grandis*, *N. pullei* and *N. resinosa*) (solid lines) shown with the temperate evergreen species from Australia (*N. moorei* and *N. cunninghamii*) (dashed lines, with *N. cunninghamii* shown by c).

( $g_s$  reduction%) was negatively correlated with  $g_{s \max}$  across species (Table 4), but there was no significant difference in the initial regression slope of  $g_s$  against time among groups ( $P > 0.05$ ) (Fig. 1a). However, the initial slope of  $g_s$  against time was higher in tropical species and *N. moorei* (suggesting higher stomatal sensitivity) than in *N. cunninghamii* (Fig. 1b), and pilot studies indicated that the reduction in conductance observed at 20 min had already occurred in the tropical species and *N. moorei* by 5–10 min.

There was less variation among tropical species in the measured variables than among temperate evergreen species and among deciduous species (Fig. 2). For example, final RWC was 72–82% in tropical species ( $I_{120-\min} = 0–11\%$ ), compared with 45–80% ( $I_{120-\min} = 7–60\%$ ) in temperate evergreen species and 19–51% ( $I_{120-\min} = 44–87\%$ ) in deciduous species. In particular, *N. moorei* and *Nothofagus menziesii* were unusual in the temperate evergreen group in reducing  $g_s$  quickly (Figs 1 & 2), so that values of RWC were similar to those of tropical species, including *Castanopsis acuminatissima* (Fig. 2). There

**Table 3** Water relations variables of tropical and temperate *Nothofagus* species derived from experimental dehydration of detached leaves.

	Tropical	Temperate		F	P
		Evergreen	Deciduous		
Conductance experiment:					
Maximum stomatal conductance, $g_{s \max}$ (mmol m <sup>-2</sup> s <sup>-1</sup> ) <sup>P</sup>	91 ± 3 <sup>a</sup>	117 ± 11 <sup>a</sup>	173 ± 14 <sup>b</sup>	11.0	< 0.001
Stomatal conductance at 20 min., $g_{s \ 20 \ min}$ (mmol m <sup>-2</sup> s <sup>-1</sup> )	21 ± 3 <sup>a</sup>	46 ± 7 <sup>b</sup>	96 ± 10 <sup>c</sup>	31.3	< 0.001
Percentage conductance of maximum, $g_{s \ 20 \ min}$	23 ± 3 <sup>a</sup>	38 ± 4 <sup>b</sup>	55 ± 4 <sup>c</sup>	20.3	< 0.001
Relative water content after 120 min., RWC <sub>120-min</sub> (%) <sup>P</sup>	77 ± 1 <sup>a</sup>	60 ± 5 <sup>b</sup>	34 ± 5 <sup>c</sup>	34.9	< 0.001
Index of injury after 120 min., $I_{120-min}$ (%)	6 ± 1 <sup>a</sup>	34 ± 5 <sup>b</sup>	69 ± 7 <sup>c</sup>	42.4	< 0.001
Pressure–volume curves:					
Water potential at relative water content = 80%, $\Psi_{RWC-80}$ (MPa) <sup>P</sup>	-1.6 ± 0.2 <sup>a</sup>	-2.3 ± 0.2 <sup>b</sup>	-1.3 ± 0.2 <sup>a</sup>	8.2	0.004
Osmotic potential at full turgor, $\Pi_{100}$ (MPa) <sup>P</sup>	-1.1 ± 0.2 <sup>a</sup>	-1.7 ± 0.1 <sup>b</sup>	-1.5 ± 0.1 <sup>ab</sup>	4.9	0.022
Osmotic potential at turgor-loss point, $\Pi_0$ (MPa) <sup>P</sup>	-1.3 ± 0.2 <sup>a</sup>	-2.2 ± 0.2 <sup>b</sup>	-1.9 ± 0.1 <sup>ab</sup>	6.1	0.011
Relative water content at turgor-loss point, RWC <sub>0</sub> (%) <sup>P</sup>	85 ± 2 <sup>a</sup>	86 ± 1 <sup>a</sup>	80 ± 1 <sup>b</sup>	6.2	0.010
Bound water, B (%) <sup>P</sup>	28 ± 3 <sup>ab</sup>	31 ± 4 <sup>a</sup>	14 ± 4 <sup>b</sup>	4.7	0.025
Bulk elastic modulus, $\epsilon$ (MPa) <sup>P</sup>	14.3 ± 4.6 <sup>a</sup>	8.8 ± 0.8 <sup>a</sup>	9.2 ± 2.7 <sup>a</sup>	1.1	0.349
Dry mass:turgid mass	0.31 ± 0.01 <sup>ab</sup>	0.35 ± 0.01 <sup>a</sup>	0.29 ± 0.02 <sup>b</sup>	4.5	0.028
Index of injury (I) at turgor-loss point (%)	5 ± 3 <sup>a</sup>	13 ± 3 <sup>ab</sup>	15 ± 1 <sup>b</sup>	4.1	0.037 <sup>L</sup>
Relative water content at I = 20%, RWC <sub>I-20</sub> (%)	67 ± 5 <sup>a</sup>	76 ± 4 <sup>a</sup>	77 ± 2 <sup>a</sup>	1.4	0.288
Relative water content at I = 50%, RWC <sub>I-50</sub> (%) <sup>P</sup>	41 ± 3 <sup>a</sup>	57 ± 4 <sup>b</sup>	55 ± 2 <sup>ab</sup>	5.2	0.018
Water potential at I = 50%, $\Psi_{I-50}$ (MPa) <sup>P</sup>	-5.4 ± 0.7 <sup>a</sup>	-4.6 ± 0.5 <sup>ab</sup>	-3.1 ± 0.1 <sup>b</sup>	5.1	0.019

Data presented are means ± SE of five to seven species' means, with the results of one-way ANOVA with post hoc Tukey's test (shared alphabet letters indicate no significant difference).

<sup>L</sup>Indicates that data were log-transformed for analysis. <sup>P</sup>Indicates traits included in the principal components analysis (Fig. 3).

**Table 4** Correlations among some water relations variables derived from the conductance and pressure–volume curve experiments (*n* = 19 species).

	$\Pi_{100}$	$\Pi_0$	RWC <sub>0</sub>	$\epsilon$	B	RWC <sub>I-50</sub>	$\Psi_{I-50}$	DM:TM	$g_{s \ max}$
$\Pi_0$	0.96***								
RWC <sub>0</sub>	-0.01	0.11							
$\epsilon$	-0.26	-0.21	0.13						
B	0.09	0.03	0.55*	-0.18					
RWC <sub>I-50</sub>	-0.68**	-0.70**	-0.07	0.02	-0.12				
$\Psi_{I-50}$	-0.39	-0.37	-0.39	0.15	-0.58**	0.64**			
DM:TM	-0.52*	-0.40*	0.30	0.17	0.29	0.21	-0.33		
$g_{s \ max}$	-0.17	-0.28	-0.57*	-0.21	-0.51*	0.19	0.46	-0.40	
$g_s$ reduction%	0.22	0.35	0.47*	0.11	0.37	-0.34	-0.44	0.07	-0.67**

Data presented are Pearson correlations with asterisks indicating the level of significance: \**P* < 0.05; \*\**P* < 0.01; \*\*\**P* < 0.001.

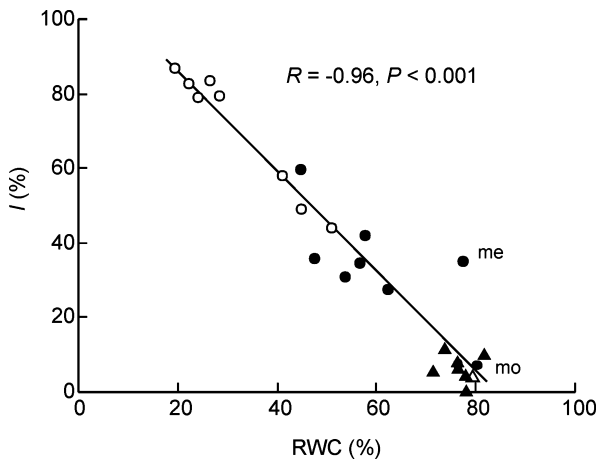
$g_s$  reduction% is the percentage reduction in  $g_s$  at time 20 min; DM:TM is the ratio of dry mass:turgid mass; other terms are defined in the text and Table 3.

was a strong negative linear relationship between  $I_{120-min}$  and RWC after 2 h dehydration across species (Fig. 2), suggesting a similar relationship between damage and water content among these species. An exception was *N. menziesii*, which was more damaged at moderate levels of water deficit than other species (Fig. 2).

**Pressure–volume curves**

The Australian evergreen *Nothofagus* species, particularly *N. cunninghamii*, developed lower water potentials than the tropical species as RWC decreased. For example,  $\Psi$  values at

RWC of 80% ( $\Psi_{RWC-80}$ ) were lower in *N. cunninghamii* (-3.3 MPa) and *N. moorei* (-2.7 MPa) than the tropical species (-0.8 to -2.1 MPa). This appeared to be a general trend, with  $\Psi_{RWC-80}$  being lower in temperate evergreen species than in tropical species (Table 3). Temperate evergreen species had significantly lower values of  $\Pi_{100}$  and  $\Pi_0$  than tropical species, but no significant difference was recorded in RWC<sub>0</sub> or B (Table 3). Deciduous species had significantly lower RWC<sub>0</sub> than either group of evergreen species and lower B than temperate evergreen species (Table 3). Dry mass:turgid mass (DM:TM) differed only between temperate evergreen and deciduous species (Table 3).



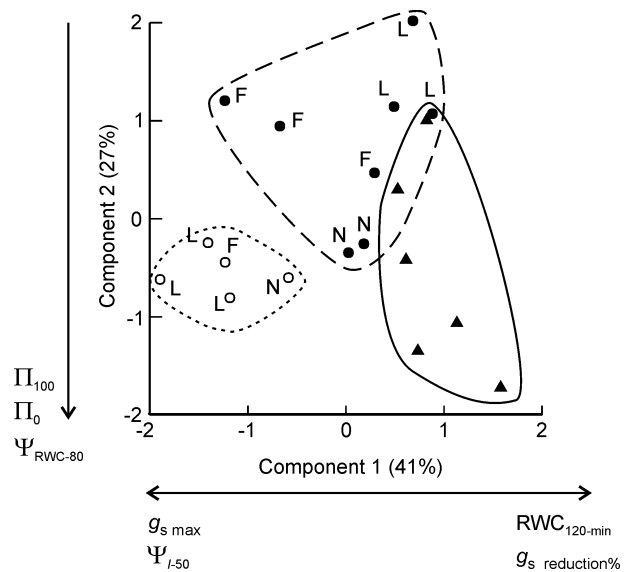
**Figure 2** The relationship between tissue damage ( $I$ ) and relative water content (RWC) in detached *Nothofagus* leaves after 120 min: ▲, tropical species; ●, temperate evergreen species; ○, deciduous species; Δ, *Castanopsis acuminatissima*; me, *N. menziesii*; mo, *N. moorei*. The data points represent the means of one to three plants per species, or the means of multiple populations (*N. pullei*, *N. moorei* and *N. cunninghamii*) or varieties (*N. solandri*). The result of Pearson correlation is given (not including *C. acuminatissima*). The line of best fit is derived by Model 1 regression.

### Effects of RWC and $\Psi$ on leaf damage

There was no significant difference in the RWC at  $I = 20\%$  ( $RWC_{I-20}$ ) among *Nothofagus* groups (Table 3). However, RWC at  $I = 50\%$  ( $RWC_{I-50}$ ) was relatively low in tropical species (with low values of tissue injury,  $I$ , at the turgor-loss point), with no difference between temperate evergreen and deciduous species (Table 3). The highest values of  $RWC_{I-50}$  among temperate evergreen species were recorded in New Zealand species (62–73%, compared with 40–53% in species from Australia and South America). This trend was consistent with relatively high values of  $\Psi_{I-50}$  in New Zealand species (−2.6 to −4.8 MPa), compared with other temperate evergreen species ( $\leq -5$  MPa). Indeed,  $\Psi_{I-50}$  and  $RWC_{I-50}$  correlated positively across species (Table 4). Deciduous species also had high values of  $\Psi_{I-50}$  (Table 3). *Nothofagus cunninghamii* had higher values of  $RWC_{I-50}$  (53%) than *N. moorei* (44%), reflecting its development of low water potentials per unit decline in RWC.

### Correlations among water relation traits across species

At the species level,  $\Pi_{100}$  and  $\Pi_0$  were negatively correlated with  $RWC_{I-50}$  (Table 4), i.e. on average, species with low osmotic potentials were less able to tolerate low RWC.  $RWC_0$  correlated positively with  $B$  and negatively with  $g_{s \max}$  and  $B$  correlated negatively with  $\Psi_{I-50}$  and  $g_{s \max}$  (Table 4). Principal components analysis showed separation of the three *Nothofagus* groups, with 68% of the variation explained by the first two components (Fig. 3). Component 1 was most strongly correlated with resistance to water loss ( $-g_{s \max}$ ,  $RWC_{120\text{-min}}$



**Figure 3** Principal components analysis configuration plot of the water relations variables. The variables included are indicated in Table 3, together with the percentage reduction in stomatal conductance ( $g_s$ ) at time 20 min. The percentage of total variance explained is given for each component, with the variables contributing most to each component (component loadings  $\geq 0.8$ ). ▲, tropical species; ●, temperate evergreen species; ○, deciduous species. L, subgenus *Lophozonia*; F, subgenus *Fuscospora*; N, subgenus *Nothofagus*; all the tropical species are in subgenus *Brassospora*. The data points represent the means of one to five plants per species, or the means of multiple populations (*N. pullei*, *N. moorei* and *N. cunninghamii*) or varieties (*N. solandri*).

and percentage reduction in  $g_s$  at 20 min) and tolerance of low water potentials ( $-\Psi_{I-50}$ ) (Fig. 3). The deciduous and tropical groups were separated along this axis, with the temperate evergreen species intermediate and overlapping the other groups. Component 2 correlated most strongly (negatively) with osmotic potentials at full and zero turgor and water potential at 80% RWC (Fig. 3). The tropical and temperate evergreen groups spread broadly along this axis, with some overlap. The species from subgenus *Fuscospora* and *Lophozonia* were relatively broadly spread across the PCA configuration plot, but the subgenus *Nothofagus* species (*Nothofagus antarctica*, *Nothofagus dombeyi* and *Nothofagus betuloides*) were located together, even though they include both evergreen and deciduous groups (all from southernmost South America) (Fig. 3). The relative importance of phylogenetic relatedness is difficult to distinguish from that of similar environments in accounting for the similarity among these species and among those of subgenus *Brassospora*.

### Root biomass allocation

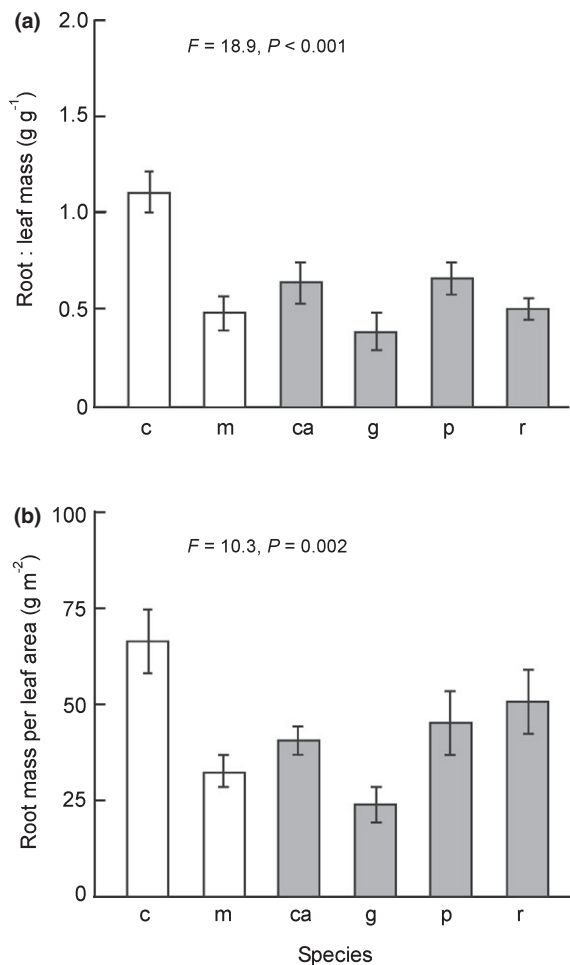
*Nothofagus moorei* and species native to New Guinea had lower root:leaf mass and root mass per unit leaf area than *N. cunninghamii* (Fig. 4).



## DISCUSSION

## Comparisons of tropical and temperate evergreen species

Tropical species of *Nothofagus* differed in water relations from temperate evergreen species in several ways. First, stomatal conductance ( $g_s$ ) dropped quickly to low levels in detached leaves of tropical species and consequently high water content was maintained and damage minimized. Stomatal sensitivity (e.g. Oren *et al.*, 1999) was not measured, but is likely to be higher in the tropical species on average, given the higher percentage decline in stomatal conductance whilst maintaining high relative water contents. This means of delaying dehydration is commonly recorded in rain forest species from particularly wet environments (Bannister, 1986; Slot & Poorter, 2007), and was recorded in *N. aequilateralis* as well as in New Guinea species, and in a few temperate species. However,



**Figure 4** Root biomass allocation in *Nothofagus* species from Australia (open bars) and New Guinea (shaded bars): c, *N. cunninghamii*; m, *N. moorei*; ca, *N. carrii*; g, *N. grandis*; p, *N. pullei*; r, *N. resinosa*. Results are given of planned contrasts between *N. cunninghamii* ( $n = 20$ ) and species from summer-high or ever-wet rainfall regimes (all other species,  $n = 6$ – $20$ ).

while resistance to water loss by rapid stomatal closure may be a particularly effective mechanism to delay tissue water deficits during unusual or mild periods of drought, it may overly constrain carbon gain in light-demanding species if water deficits are common. Second, the tropical species showed a lesser capacity than temperate evergreen species to develop low water potentials as water content declined, a mechanism of delaying dehydration that is common in drought-resistant plants (Jarvis & Jarvis, 1963; Hsiao *et al.*, 1976; Turner, 1986).

The tropical species did not exhibit the poor tolerance of water deficits that often accompanies high resistance to water loss (Bannister, 1986), instead showing similar or higher desiccation tolerance (judged by  $RWC_{-20}$ ,  $RWC_{-50}$  and  $\Psi_{-50}$ ) to that of temperate evergreen and deciduous species. The tropical species also showed similar values of percentage bound water and the bulk elastic modulus to temperate species. This suite of traits suggests that although soils rarely dry to a significant degree across the distribution of the New Guinea species, and humidity is typically high (Ash, 1982; Read *et al.*, 2005), these species may experience short-lived periods of moderate vapour pressure deficit.

The temperate evergreen species on average showed traits more typical of 'water-spenders', with higher rates of conductance in drying leaves and a greater capacity to delay tissue water deficits by reducing water potential relative to water content, with low  $\Pi_{100}$  and  $\Pi_0$ . Low osmotic potentials have been recorded in temperate evergreen *Nothofagus* species in previous studies (Körner & Bannister, 1985; Bannister, 1986; Somerville & Read, 2008). The temperate evergreen species commonly experience cool to cold winters combined with winter-high rainfall regimes (excluding *N. moorei*) (Table 1; and interpreted from Maunder, 1971; Miller, 1976; and Prohaska, 1976), or at least rainfall regimes in which mild to moderate water deficits may be experienced in summer when evaporation rates are higher, especially on shallower soils (e.g. Wardle, 1991). For example, *Nothofagus solandri* var. *cliffortioides* (Wardle, 1984) and *N. dombeyi* (Weinberger, 1973) extend onto sites likely to experience summer water deficits, and species may experience winter desiccation on exposed cold and dry sites (Wardle, 1984). However, the magnitude and form of water deficits experienced by some temperate *Nothofagus* species is uncertain, particularly those occurring in regions of high summer rainfall, e.g. southernmost Chile (Miller, 1976) and parts of the South Island of New Zealand (Maunder, 1971).

The ranges of values of water relations variables were generally similar to those recorded in comparable trees from other studies (e.g. Cheung *et al.*, 1975; Larcher, 2003), including studies of *Nothofagus* (Cheung *et al.*, 1976; Jane & Green, 1983; Bannister, 1986; Bannister & Kissel, 1986; Sun *et al.*, 1995). Values for individual species were sometimes at the margins of the typical range of values recorded in temperate forest trees. For example,  $\Pi_0$  was low ( $-3.0$  to  $-3.2$  MPa) in some populations of *N. cunninghamii* and *N. solandri* var. *cliffortioides*. However, these traits were not paired with high tolerance of desiccation, indicating that drought resistance is limited in these species compared with species

adapted to drier environments. Few data are available to indicate whether low minimum values of  $\Psi$  recorded experimentally also occur under field conditions in these species, or to indicate the importance of acclimation, e.g. osmotic adjustment, under field conditions.

### Comparisons of Australian evergreen species

The Australian evergreen species showed a particularly interesting contrast with each other and with the New Guinea species. *Nothofagus moorei* experiences summer-high rainfall on average, but more pronounced temperature seasonality than the tropical species and lower rainfall (annual and seasonal) (Table 1). Consistent with its slightly higher long-term water-use efficiency than *N. cunninghamii* under common (well-watered) conditions (Read & Farquhar, 1991), *N. moorei* reduced conductance quickly in detached leaves ( $g_{s\ 20\text{-min}} = 27\%$ ), so that water content remained high, with little tissue damage, similar to that of the tropical species. *Nothofagus cunninghamii* reduced conductance more slowly ( $g_{s\ 20\text{-min}} = 54\%$ ), leading to greater water loss and damage. However, *N. cunninghamii* developed lower water potentials per unit decrease in water content ( $\Psi_{\text{RWC}_{-80}} = -3.3$  MPa compared with  $-2.7$  MPa in *N. moorei*), and so under field conditions, i.e. without leaf detachment, can potentially maintain the rates of water uptake needed to maintain tissue water status and photosynthetic rates. The capacity of *N. moorei* to develop lower water potentials per unit decrease in water content than the tropical species may reflect its occurrence in areas that may be more prone to water deficits.

A rain forest species such as *N. cunninghamii* that maintains high rates of conductance and potentially photosynthesis (Cunningham, 2005) during warm but relatively drier conditions, without high tolerance of tissue desiccation, requires high rates of water uptake. Consistent with this, *N. cunninghamii* also has a higher mass allocation to roots relative to leaf mass and area than *N. moorei* and the tropical species. However, investment in osmotically active compounds and a high root:leaf ratio presents opportunity costs to growth, and our data suggest that these costs are incurred even under well-watered conditions. Therefore, it is unlikely, even under ideal growth conditions, that *N. cunninghamii* could achieve the growth rates of the tropical species, which seem to be using relatively low-cost mechanisms of drought resistance targeted at mild vapour pressure deficits of short duration, with *N. moorei* intermediate. This investment is likely to limit the competitiveness of *N. cunninghamii* (via carbon balance and growth rates) at lower latitudes that experience higher summer rainfall. Similar limitations are likely in other temperate *Nothofagus* species native to climates that experience summer water deficits.

### Contrasts in water relations between evergreen and deciduous habits

The deciduous species typically showed high maximum rates of stomatal conductance and maintained high levels of conduc-

tance as leaves dehydrated, leading to low relative water contents (about half that of the evergreen species) and greater damage. The deciduous species may also have higher cuticular permeance (e.g. Burghardt & Riederer, 2003). However, there was little evidence of compensatory tolerance mechanisms for the high rates of water loss, other than a slightly lower water content at zero turgor:  $\text{RWC}_{I-20}$  and  $\text{RWC}_{I-50}$  were similar to temperate evergreen species, but  $\Psi_{I-50}$  was higher in deciduous species, and South American deciduous species were more damaged ( $\text{RWC}_{I-20} = 73\text{--}81\%$ ;  $\text{RWC}_{I-50} = 50\text{--}60\%$ ) than evergreen species from the same region ( $\text{RWC}_{I-20} = 57\text{--}64\%$ ;  $\text{RWC}_{I-50} = 40\text{--}45\%$ ).

Hence the deciduous species appear to have lower physiological drought resistance than temperate evergreen species (including evergreen species from the same region) and tropical species, based on the measured traits. Opposite trends have been found among some Mediterranean *Quercus* species, with rapid stomatal closure in deciduous, but not evergreen, species (Acherar & Rambal, 1992). In that case, however, the evergreen species extended to drier climates than the deciduous species. In other studies (e.g. Sobrado, 1986; Jackson *et al.*, 1995), the deciduous species investigated are leafless during the dry season, unlike the case in *Nothofagus*. In *Nothofagus*, some deciduous species extend to relatively dry environments (summer-dry) (Weinberger, 1973; McQueen, 1976): *Nothofagus obliqua* and *Nothofagus glauca* occur in warm temperate deciduous forests in the mediterranean-type climatic region of central Chile (Donoso, 1996), and *N. antarctica* occurs on cool dry sites on the eastern Andes near the Patagonian steppe ecotone (Veblen *et al.*, 1996b). Like the high-latitude evergreen species, but with even greater imperative given winter leaflessness, deciduous species must maximize photosynthetic opportunities during the summer period. Hence, a water-spending habit is not unexpected in deciduous species from either wetter or drier climates, but how it is supported on dry sites is unclear. It is likely there are differences in unmeasured morphological traits, such as mass allocation to roots and root architecture (Hinckley *et al.*, 1983; Bucci *et al.*, 2009), or in physiological traits including hydraulic characteristics (Larcher, 2003; Bucci *et al.*, 2009), that explain these patterns. The capacity to drop leaves in severe drought may contribute to survival of these deciduous species (and possibly some evergreen species) in unusually dry years. We also note that drought resistance may have been under-estimated for some species if ecotypic variation occurs along climatic gradients, since we have not sampled populations from dry regions.

### Comparative drought resistance among and within *Nothofagus* groups

Even though these species commonly occur in regions of high rainfall, drought damage has been reported in *Nothofagus* in New Guinea (Brown & Powell, 1974), New Zealand (Wardle, 1984, 1991) and southern South America (Veblen *et al.*, 1996b; Suarez *et al.*, 2004), including in species that typically experience high annual and summer rainfall. Hence, rain forest species may experience both mild water deficits on a regular basis and severe water deficits during drought years. For the

Australian species, wildfire may provide a more direct constraint at the drier end of their range (Read & Brown, 1996), and fire may influence the distributions of *Nothofagus* species elsewhere (Veblen *et al.*, 1999; Ledgard & Davis, 2004).

While some differences in strategies of these groups of *Nothofagus* are clear, the comparative drought resistance (capacity to survive drought) of the *Nothofagus* groups is not clear. Few data are available on field responses to drought conditions for these species, and the climate estimates presented for species from Australia and New Guinea that might allow prediction of drought resistance of the groups do not fully reflect water availability. The latter will be influenced by factors such as evapotranspiration, soil properties (including depth) and water-use traits of co-occurring species, and water availability may exert indirect effects via fire regimes. We did not expose intact seedlings to soil water deficits or measure traits such as root signalling or hydraulic resistance (Tyree *et al.*, 1991, 1999), stem water storage (Goldstein *et al.*, 1998) or root profiles (Moreno-Chacón & Lusk, 2004); nor have we compared the functional characteristics of adult trees, including roles of root grafts (observed in *N. cunninghamii*: Packham, 1994) and mycorrhizae in water uptake. In addition, drought resistance may be conferred by differing but overlapping suites of traits (e.g. Bannister & Kissel, 1986). Nevertheless, drought tolerators are usually viewed as being better adapted to conditions of moderate drought stress than drought avoiders (Bannister, 1986; White *et al.*, 2000), and our data suggest that the tropical species would probably be outcompeted by temperate species such as *N. cunninghamii* in a climate having temperature seasonality paired with lower summer rainfall.

Part of the difficulty in predicting comparative drought resistance among these groups of species lies in the varying nature of drought regimes, with even co-occurring species varying in water relations (e.g. Jackson *et al.*, 1995; Bonal & Guehl, 2001; Somerville & Read, 2008). Considerable variation in water relations occurs among species within latitudinal zones, given that species vary in distribution with respect to climate at this finer scale (e.g. Engelbrecht *et al.*, 2007). However, we noted relatively little variation among the tropical species in some traits compared with that observed within each of the temperate groups (e.g. Fig. 2), reflecting greater variation in climate regimes experienced by the temperate species. For example, detached leaves of *N. menziesii* maintained a relatively high water content, consistent with previous evidence of a conservative water strategy, with high sensitivity of stomata to ambient humidity (Körner & Bannister, 1985; Bannister, 1986; Sun *et al.*, 1995). *Nothofagus solandri* var. *cliffortioides* showed relatively low  $\Pi_{100}$  and  $\Pi_0$ , consistent with its common replacement of *N. menziesii* on drier (and sometimes shallow soils) (Wardle, 1984; Sun *et al.*, 1995; Ogden *et al.*, 1996). We note in particular the potential evolutionary role of 'recent' historical factors in some responses to water stress. *Nothofagus cunninghamii* is suggested to have occurred in Pleistocene refugia that were colder (McKenzie, 1995) and possibly drier (Worth *et al.*, 2009) than currently experienced. The climate regime currently experi-

enced by *N. cunninghamii* is probably limited by a fire regime that may not have been so restrictive in a cooler Pleistocene climate. Nevertheless, some traits may partly reflect the conditions of Pleistocene refugia.

### Are these generalized trends?

It is uncertain whether the trends recorded between tropical and temperate *Nothofagus* species occur widely across other taxa and regions. Relatively few studies have investigated water relations in tropical and temperate species of similar niche grown under common conditions. Indeed, given the known variation in ecology among rain forest species within a region (Bannister, 1986; Bannister & Kissel, 1986; Somerville & Read, 2008), and of the variation in rainfall seasonality and related climate variables within regions (e.g. Malhi *et al.*, 1999), perhaps similar trends should not be expected. Furthermore, since *Nothofagus* species in New Guinea are generally confined to forests at mid to high altitudes, they may experience lower vapour pressure deficits than lowland rain forest species, so trends in *Nothofagus* may not be typical of tropical lowland species. Indeed, some overlap in traits between temperate and tropical species may reflect overlapping environments due to moderating effects of elevation on temperature regimes and atmospheric and soil water availability. We also note that evolutionary trends in *Nothofagus* may have been constrained by ancestral traits; other taxa may show different trends. For example, lower maximum water-use efficiency has been recorded in conifers from wet tropical New Guinea and New Caledonia than in conifers from wet temperate regions (Brodribb & Hill, 1998).

Nevertheless, some similar responses have been recorded in other studies. Cunningham (2004, 2005) found that Australian tropical rain forest canopy species showed higher stomatal sensitivity to vapour pressure deficits and greater decreases in net photosynthesis than temperate rain forest species. Similarly, Park & Furukawa (1999) recorded greater sensitivity of tropical trees than temperate trees to vapour pressure deficits in terms of stomatal conductance and net photosynthesis. Hence some water relations traits may be more common in tropical than temperate habitats of particular forest types, at least when comparing species of similar niche, due to differences in water regimes combined with differences in temperature seasonality.

### CONCLUSIONS

Differences in water relations were found among the *Nothofagus* groups that appear to reflect differences in climate regimes. In particular, species experiencing ever-wet rainfall regimes in New Guinea and summer-high regimes in mid-latitude Australia showed water conservation traits that were unlikely to have substantial opportunity costs to growth in these climates. In contrast, high-latitude evergreen species on average invested more in maximizing water uptake. This was particularly evident in the Australian species *N. cunninghamii*, which developed low

water potentials and high root:leaf biomass, potentially allowing carbon assimilation to be maximized during the warmer summer months. However, this strategy, while probably maximizing growth in its temperate environment with cool winters, must constrain its capacity to compete at lower latitudes via effects on carbon balance and growth. Hence it is likely that responses to water regimes contribute substantially to the equatorward distributions of some evergreen species, not temperature regimes alone. In particular, this behaviour differentiates *N. cunninghamii* more strongly from the closely related mid-latitude temperate species *N. moorei* than responses to temperature (Read, 1990). Conversely, the water-relations traits shown by extant tropical and mid-latitude species may have contributed to loss of their relatives from south-eastern Australia from the mid-Miocene into the Plio-Pleistocene when climates were becoming cooler and drier, but more seasonal in both temperature and rainfall, and with a shift at some stage to summer-low rainfall. These results provide further evidence that the poleward distribution of species may be proximally constrained by competitive interaction via effects of water relations and other aspects of physiology on carbon balance, rather than by climatic 'intolerance' per se. Investigation of other plant traits, for example in relation to hydraulic conductivity, root allocation and architecture, and acclimation to water stress, in addition to studies of diurnal and seasonal patterns under field conditions, in a wider range of species, would be of value in further exploring trends between tropical and temperate species.

## ACKNOWLEDGEMENTS

This research was funded by the Australian Research Council and a Monash Small Grant. We thank staff of the Department of Forests, Papua New Guinea, for assistance collecting seedlings in Papua New Guinea, and A. Floyd, J. Williams (deceased) and C. Bale for advice regarding collection of *N. moorei* seedlings. Permission to collect seedlings was given by the Papua New Guinea Department of Forests, the NSW Department of Environment, Climate Change and Water, Department of Sustainability and Environment, Victoria, and the Department of Primary Industries, Water and Environment, Tasmania. We are grateful to A. Floyd (North Coast Regional Botanic Gardens Herbarium) and the NSW Department of Environment, Climate Change and Water for additional location data for *N. moorei*. We thank C. Beadle for helpful comments on an early draft.

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Editor: Eileen O'Brien